Pergamon

0042-6989(95)00277-4

*Vision Res.*, Vol. 36, No. 20, pp. 3311–3323, 1996

Printed in Great Britain
0042-6989/96 $15.00 + 0.00

# Perceptual Stability and the Selective Adaptation of Perceived and Unperceived Motion Directions

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*Received 7 October 1994; in revised form 20 May 1995*

**Adaptation was studied in a paradigm in which the adapting stimulus was a variably biased version of a bistable apparent motion stimulus, a motion quartet, and the post-adaptation test stimulus was a "neutral" motion quartet. Either horizontal or vertical motion was perceived, never both at the same time. When only one of these was perceived during the entire adaptation phase of a trial, and the perceived motion was highly stable, adaptation effects were greater for the perceived than the unperceived motion directions (i.e., adaptation was selective to the perceived motion). However, when the perceived motion during adaptation was relatively unstable (i.e., when the perceived motion was more likely to spontaneously change directions), similar levels of adaptation were obtained for perceived as well as unperceived, but possible motion directions. Thus, adaptation occurs prior to the determination of which of the competing motion directions will be perceived. The relationship between the stability of the adapting percept and the selectivity of adaptation is explained in terms of differences in the activation of mutually inhibitory horizontal and vertical motion detectors. Copyright © 1996 Elsevier Science Ltd.**

Selective adaptation Stability Apparent motion Motion directionality Bistability

## INTRODUCTION

Selective adaptation is among the most extensively documented phenomena in vision research. Some classical examples involve the effect of prolonged exposure to suprathreshold, high contrast sine gratings on sensitivity to sine gratings presented at threshold level contrasts. Decreased sensitivity (threshold elevation) is obtained, but the effect of adaptation is selectively linked to specific attributes of the adapting grating. Thus, adaptation effects are observed only if the adapting and test stimuli are similar in spatial frequency and orientation (Blakemore & Campbell, 1969; Pantle & Sekuler, 1968). In some studies, the effects of adaptation are only partially selective. For example, if an adapting grating is moving, contrast sensitivity is decreased more when test gratings are moved in the adapting than in the opposite direction (Sekuler & Ganz, 1963), but there is also some reduction in contrast sensitivity in the opposite direction (Levinson & Sekuler, 1975; Pantle & Sekuler, 1969).

Selective adaptation has also been studied for more complex patterns, but now instead of observing the effect of the adapting stimulus on detection thresholds, investigators have studied the effect of the adapting stimulus on perception when viewing ambiguous, bistable figures (we refer to these as threshold adaptation and bistability adaptation paradigms, respectively). Some time ago, Hochberg (1950) studied the perceptually ambiguous Maltese cross (a circle divided into eight equal sectors of alternating black and white color). Either a black cross is seen against a white background or a white cross is seen against a black background. Perception was biased by varying the luminance of the surround. Prolonged inspection (up to 5 min) of a version biased toward the perception of one pattern (e.g., the black cross) increased the likelihood that the alternative pattern (the white cross) would be perceived when the ambiguous version of the stimulus was subsequently presented. The effect, however, was obtained only if the black cross was in the same orientation during the adaptation and test phases of the experiment. More recently, Nawrot & Blake (1989) studied the perceived direction of three-dimensional rotation for the two-dimensional projection of spots of light on a rotating, transparent sphere. Following prolonged exposure to a version biased such that the near surface perceptually rotated to the left, the perceived rotation for an unbiased test sphere tended to be to the right, providing the rotation axis was the same during adaptation and test.

Kruse *et al.* (1986) have provided evidence for selective adaptation effects with motion quartets. These

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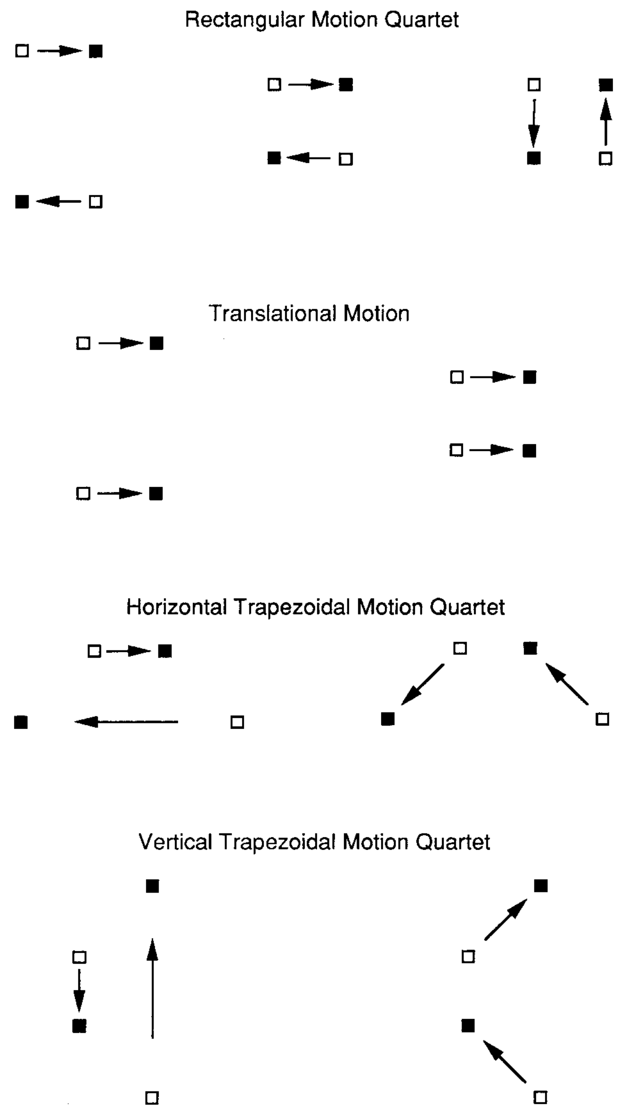



FIGURE 1. Illustration of the apparent motion stimuli presented in this study and the motion patterns that are perceived for each. The open and solid squares indicate the dot positions on odd- and even-numbered frames, respectively. Only horizontal motion is perceived for the rectangular motion quartet with the large aspect ratios; either horizontal or vertical motion can be perceived for the rectangular motion quartets with aspect ratios near 1.0. Rectangular motion quartets with different aspects ratios were presented during the adapting phases of Experiments 1–4; rectangular motion quartets with aspects ratios near 1.0 were presented during the post-adaptation, test phases of Experiments 1, 2, 3 and 5. The translation motion stimuli were presented during the adaptation phase of Experiment 2. Only horizontal motion was perceived for these stimuli, regardless of their aspect ratio. The trapezoidal quartets were presented during the post-adaptation, test phase of Experiment 4 and the adaptation phase of Experiment 5. The perception of oblique motion competed with the perception of either horizontal motion (for the horizontally oriented, trapezoidal quartets) or vertical motion (for the vertically oriented, trapezoidal quartets).

*Activation level and reduced sensitivity are typically associated with the intensity of stimulus attributes. For example, the brighter the adapting stimulus, the greater the reduction in light sensitivity (Mueller, 1951), and the greater the adapting contrast, the greater the reduction in contrast sensitivity (Blakemore & Campbell, 1969).

apparent motion stimuli are formed by simultaneously presenting two points of light corresponding to the diagonally opposite corners of an imaginary rectangle, then simultaneously presenting the two points of lights corresponding to the other diagonally opposite corners, then the first pair again, then the second pair again, and so on. Both dots are perceived to move vertically, though in opposite directions, or both dots are perceived to move horizontally, again in opposite directions (see top of Fig. 1). Kruse and colleagues' adapting quartet had an aspect ratio (vertical/horizontal distance between the dot positions) of 2.26, which strongly favors the perception of horizontal motion. The effect of prolonged viewing of this biased adapting quartet was to increase the likelihood of vertical motion being perceived for the subsequently presented, neutral test quartet (its aspect ratio was 1.13). Kruse *et al.* (1986) found that adaptation was strongest when the temporal frequency of the test quartet was the same as that of the adapting quartet.

In all these cases, it is assumed that the effect of adaptation is to reduce the sensitivity of detectors selective to one of the alternative percepts, and thereby, to reduce their activation by the subsequently presented, unbiased test stimulus.* We have further investigated adaptation effects in the motion quartet paradigm for two reasons. The first is that even for highly biased versions of the motion quartet, it is likely that both horizontal and vertical motion detectors are activated. For example, when the aspect ratio of the motion quartet strongly biases the percept to favor horizontal motion, vertical motion will rarely, if ever, be perceived. However, vertical motion is always perceived when the same apparent motion stimulus is presented in a non-competing situation, i.e., when the alternating pair of dots is not embedded in the motion quartet and is displaced by the same vertical distances that result in a strong bias against the perception of vertical motion within the motion quartet. Therefore, it is likely that detecting units for both horizontal and vertical motion are stimulated simultaneously by motion quartets, though the perceived motion is either horizontal or vertical, never both at the same time. On this basis it was possible to ask whether adaptation is selective to the perceived motion directions, or whether adaptation effects can also occur for the unperceived motion directions.

The second reason for studying adaptation effects with motion quartets is that unlike other stimuli used in the bistability adaptation paradigm, the biased and neutral versions of the motion quartet lie along a well-defined continuum. Previous studies (Hock *et al.*, 1993; Hock & Voss, 1990) have established that the aspect ratio of the motion quartet determines the relative stability of the perceived horizontal and vertical motion. When the aspect ratio favors one motion pattern, and that motion is perceived, the percept is more stable than if the unfavored motion pattern is perceived. This difference in stability, which decreases as the aspect ratio is closer to 1.0, is reflected in the likelihood of the perceived motion directions spontaneously changing (stable percepts are less likely to spontaneously change than unstable percepts). On this basis, we could vary the motion quartet's aspect ratio and determine whether the stability of the motion perceived during adaptation predicts selectivity in adaptation (i.e., whether adaptation effects are limited to perceived motion directions).

## EXPERIMENT 1

The key to this experiment, as well as those that follow, is that regardless of the aspect ratio of the adapting motion quartet, only the results of trials for which horizontal motion was perceived for the entire adaptation phase were evaluated. If adaptation depends only on the motion perceived during the adaptation phase of each trial, equal adaptation effects would be observable during the subsequent test phase for all the adapting aspect ratios; i.e., when horizontal motion is perceived for the entire adapting phase, the likelihood of perceiving vertical motion during the test phase would not depend on the aspect ratio of the adapting quartet.

### *Method*

*Subjects*. Two of the subjects were students at Florida Atlantic University (LH and KE). Since they were well practiced with the motion quartets, they were aware that the perception of both vertical and horizontal motion was possible.* Both, however, were naive with respect to the purpose of the experiment (as were SB, SP, and GB in subsequent experiments). The first author, also well practiced, was the third subject. All subjects had normal or corrected-to-normal vision.

*Stimuli*. Pairs of white dots were presented over a series of frames against the dark background of a Macintosh II RGB monitor. The size of each dot was one pixel, intercepting a visual angle of 1.6 min from the 80 cm viewing distance (maintained by a head restraint). The luminance of each dot was 12.8 cd/m$^2$. Each experimental trial was composed of an adaptation and test phase separated by a 390 msec blank interval. Motion quartets presented during each phase were structured into a series of two-frame display cycles: Two dots corresponding to the opposite diagonal corners of an imaginary rectangle were presented for 195 msec, then on the next frame two dots corresponding to the other diagonal corners of the imaginary rectangle were presented for 195 msec. The resulting temporal frequency, 2.6 Hz, was too slow for adaptation effects observed in this study to be attributable to the breakdown of apparent motion (Anstis *et al.*, 1985; Finlay & Von Grünau, 1987).

The horizontal distance between the dot positions was always four pixels (6.4 min visual angle). The aspect ratio of the rectangular motion quartets was varied by changing the vertical distance between the dot positions; for all aspect ratios the locations of the top two dots was the same and the vertical distance between the top and bottom dot positions varied from 4.8 to 14.4 min. The resultant aspect ratio (the vertical divided by the horizontal distance between dot positions) during the entire adaptation phase of each trial was either 0.75, 1.0, 1.25, 1.5, 1.75, 2.0 or 2.25. The aspect ratio during the entire test phase of each trial was either 1.0 or 1.25. Either horizontal or vertical motion was perceived during each phase (top of Fig. 1). In order to minimize possible inter-trial effects, an "interrupting" sequence of frames was presented at the end of each trial. The upper-left and lower-right dots of the motion quartet with an aspect ratio of 1.0 were presented in alternation for twelve 195 msec frames, resulting in a percept with a continually reversing, diagonal motion path.

Two points regarding the motion quartets are of particular importance. First, the distance over which horizontal motion was perceived was the same for all the adapting and test quartets. Thus, evidence for aspect ratio-dependent reductions in sensitivity to horizontal motion during the test phase would not be attributable to adaptation/test differences in the pathlength or the speed of the perceived horizontal motion. Second, for all the aspect ratios studied, when only the right (or left) pair of dots are presented in alternation, vertical motion is readily perceived. Thus, horizontal motion did not dominate for large aspect ratio quartets because the vertical distance between dot positions was too great for apparent motion to be seen.

The adaptation phase of each trial was composed of six two-frame display cycles, and the test phase of each trial was composed of three two-frame display cycles. Although the brief adaptation interval (2.4 sec) is not unique [e.g., Sekuler & Ganz (1963) obtained adaptation effects for 5 sec adaptation intervals], it made it possible for us to carry out the objectives of the experiment. If long adaptation intervals had been required, the rate of spontaneous switching to vertical motion during adaptation would have been too high to measure the adaptive effect of perceived horizontal motion for adapting aspect ratios close to 1.0.

*Procedure*. Subjects were instructed to look at each quartet without attempting to focus their attention on a particular location. After each trial, subjects pressed one of two keys on the computer keyboard with fingers of their left hand to indicate whether or not the perceived motion was horizontal during the *entire* adaptation phase, and then pressed one of two keys with fingers of their right hand to indicate whether or not vertical motion was perceived any time during the test phase.

*Design*. All 14 combinations of the seven adaptation aspect ratios and two test aspect ratios were presented equally often, their order randomized in blocks of 28 trials. LH participated in six testing sessions; KE and HH participated in four testing sessions (there were 8 blocks of 28 trials per session, with a variable rest period after the fourth block).

*Girgus *et al.* (1977) have found that adaptation effects in the bistability adaptation paradigm often are not obtained when subjects are unaware of the alternative to the pattern perceived during adaptation.

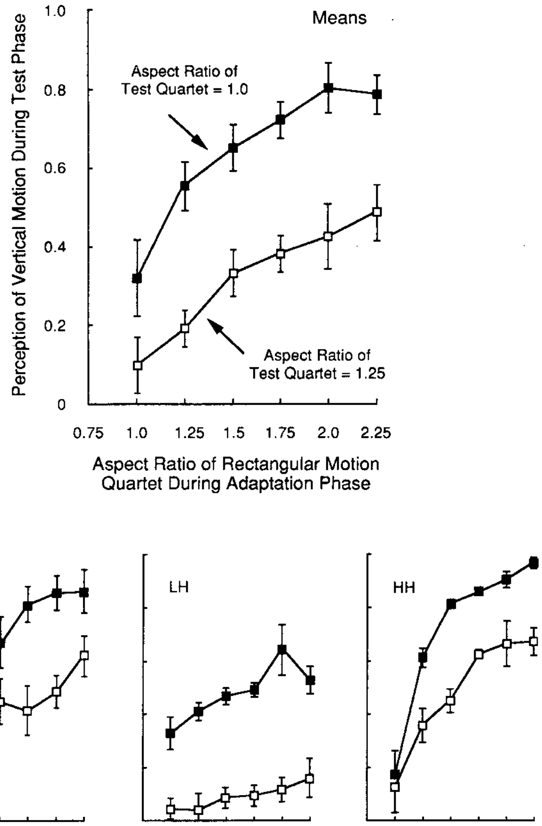



FIGURE 2. Experiment 1: The effect of the rectangular adapting quartet's aspect ratio on the proportion of trials for which vertical motion was perceived anytime during the test phase (the rectangular test quartets had aspect ratios of 1.0 or 1.25). Data are reported only for trials during which horizontal motion was perceived for the entire adaptation phase (there were too few data points when the adapting aspect ratio was 0.75 for the results to be included in the graphs). Standard errors for each subject (over sessions) and mean standard errors are indicated by error bars.

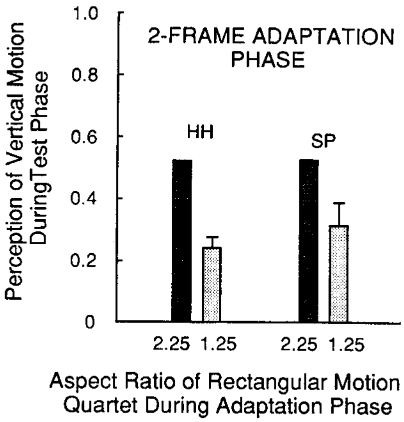



FIGURE 3. Experiment 1 (additional results): the proportion of trials for which vertical motion was perceived anytime during the test phase as a function of the aspect ratio of the two-frame adapting quartets. Data are reported only for trials during which horizontal motion was perceived for the adapting quartet (aspect ratios were 2.25 or 1.25 for the adapting quartets and 1.25 for the test quartet). Standard errors of the difference between the 2.25 and 1.25 adapting aspect ratios (over sessions) are indicated by error bars.

### *Results*

Consistent with previous studies (Hock *et al.*, 1993; Hock & Voss, 1990), horizontal motion was perceived for the entire adapting duration more often for the adapting quartets with the larger aspect ratios (averages were 98, 99, 97, 95, 80, 29, and 3% of the trials for adapting aspect ratios of 2.25, 2.0, 1.75, 1.5, 1.25, 1.0, and 0.75, respectively). Adaptation effects were measured for these trials by determining the frequency with which vertical motion was seen during the test phase. The results for all three subjects indicate that the perception of vertical motion during the test phase increased as the aspect ratio of the quartet presented during the adapting phase was increased (Fig. 2). If the perceiver's post-adaptation motion sensitivity depended only on the motion perceived during adaptation, equal effects would have been obtained in the test phase for all the adapting aspect ratios since the reported data are limited to trials for which the perceived motion during adaptation was always horizontal, regardless of aspect ratio. Furthermore, if adaptation effects were selective to the particular geometry of the pattern perceived during adaptation, there would have been more adaptation for the adapting quartets with aspect ratios near 1.0, which were geometrically the most similar to the test quartets. It was concluded, therefore, that the adaptation effect depended on the aspect ratio of the adapting quartet, but did not simply depend on the motion directions perceived during adaptation.

*Additional results.* The brevity of the adaptation interval in Experiment 1 (2.4 sec) makes it unlikely that the observed adaptation effect was the result of neural fatigue (Maffei *et al.*, 1973). To strengthen this point, an additional experiment tested for the effects of adaptation intervals of 0.4 sec, sufficient time for only a single, two-frame apparent motion sequence. Motion quartets with aspect ratios of 2.25 and 1.25 were presented for one display cycle during the adaptation phase of each trial, and as before, a quartet with an aspect ratio of 1.25 was presented for three display cycles during the test phase. The centers of the adapting stimuli corresponded with the center of the screen, and following a 495 msec blank interval, the test quartet was presented 24 min from center in one of eight randomly selected directions. Results were again analyzed only for trials in which horizontal motion was perceived during the adaptation phase. As before, vertical motion was perceived for the test quartet more often following the 2.25 compared with the 1.25 adapting quartet (Fig. 3). Given the minimal duration of the adaptation interval, it could be concluded that the adaptation effect was not the result of neural fatigue.

### *Discussion*

Visual adaptation concerns the adjustment of the visual system to the immediate conditions of stimulation. The adjustment can occur over a wide range of time scales. For example, it can involve increases and decreases in sensitivity over long time scales (e.g., dark and light adaptation), or decreases in sensitivity over a short time scale (e.g., motion adaptation; Sekuler & Ganz, 1963 as well as the current study). Gain control mechanisms (Walraven *et al.*, 1990) rather than neural fatigue are likely to be the basis for changes in sensitivity occurring over very brief adapting intervals.

Previous studies using the bistability adaptation paradigm have typically concluded that sensitivity to a pattern perceived for a bistable stimulus has been reduced (i.e., there has been an adaptation effect) when its post-adaptation frequency of perception is reduced compared with its base frequency of perception (when there is no prior adaptation). Although this kind of comparison has been successful in the threshold-adaptation paradigm (e.g., Blakemore & Campbell, 1969), it has not been introduced in the present study because of the inherent difficulty of establishing truly neutral conditions for determining base frequencies of perception for bistable stimuli. When a relatively neutral bistable stimulus is presented over a series of trials, the frequency with which a pattern is perceived is strongly influenced by hysteresis effects; i.e., the perceived pattern tends to be the same as the previously perceived pattern (e.g., Hock *et al.*, 1993), so the initially perceived pattern may dominate the measurement. The problem is not necessarily alleviated by including less neutral versions of the bistable stimulus in the test set (e.g., other aspect ratios) since the measured base frequencies of perception for a bistable stimulus are likely to vary with the particular context in which it is presented. From this point of view, the best evidence for adaptation in previous studies has come not from comparison with non-adaptation, base frequencies, but from the differential effects of a specific, adaptation-dependent parameter; e.g., selectivity to the orientation of the adapting cross in Hochberg (1950). Our conclusion that there were adaptation-dependent changes in sensitivity in Experiment 1 was based on the differential effect of the various adapting aspect ratios on the perception of vertical motion during the test phase of each trial.

## EXPERIMENT 2

If adaptation in Experiment 1 only depended on the motion perceived during the adaptation phase, equal adaptation effects would have been obtained for all the adapting aspect ratios. This was because: (1) the reported data were limited to trials for which the perceived motion during adaptation was always horizontal, regardless of aspect ratio; and (2) the aspect ratio was varied by changing the vertical distance between the dots, so the horizontal motion seen during adaptation and test was the same for all aspect ratios. The purpose of Experiment 2 was to determine whether the effect of the adapting aspect ratio was due to the activation of vertical motion detectors by the motion quartet, even though horizontal motion was being perceived.

This hypothesis was tested by comparing the adaptive effects of the horizontal apparent motion perceived with motion quartets, for which activation of vertical motion detectors is possible, to the adaptive effects of the horizontal motion perceived for purely translational apparent motion stimuli (Fig. 1). Given the $\pm 60$ deg bandwidth of directionally selective motion detectors (Ball *et al.*, 1983), activation of vertical motion detectors by the horizontal, translational stimuli is likely to be minimal. Hence, reductions in sensitivity during adaptation to the horizontal, translational stimulus would primarily involve horizontal motion detectors, and the perception of vertical motion would be enhanced during the test phase. If, however, vertical as well as horizontal motion detectors are activated by the motion quartet, reduced sensitivity to horizontal motion could be accompanied by reduced sensitivity to vertical motion (i.e., both adapt), and/or the activation of horizontal detectors (and therefore, their adaptation) could be reduced as a result of inhibitory interactions originating from the activated vertical detectors (Snowden, 1989). In either case, less perception of vertical motion would be expected for test quartets when there is more activation of vertical motion during the adaptation phase.

### *Method*

*Stimuli.* The interval between the adapting (six display cycles) and test (three display cycles) phases of each trial was 495 msec. Trials in which motion quartets were presented during adaptation were randomly interleaved with trials in which translational motion stimuli were presented during adaptation. The test stimulus was always a motion quartet. The aspect ratio of the quartets presented during adaptation was 2.25 or 1.25 (the horizontal distance between dot positions was 6.4 min and the vertical distance was either 14.4 or 8.0 min). The translational motion stimuli presented during adaptation had corresponding aspect ratios (the vertical distance between the dots was 14.4 or 8.0 min; their horizontal displacement was 6.4 min). Like the quartets, the translational stimuli were structured into a series of two-frame display cycles; two dots corresponding to the leftmost corners of an imaginary rectangle were presented for 195 msec, then the two dots corresponding to the rightmost corners of the imaginary rectangle were presented for 195 msec. The centers of all the adapting stimuli corresponded with the center of the screen, and the center of the rectangular motion quartet (aspect ratio = 1.25) presented during the test phase was displaced 24 min from center in one of eight randomly selected directions.

*Procedure.* The first response at the end of each trial indicated whether horizontal motion was perceived for the entire adaptation phase; the second indicated whether vertical motion was perceived anytime during the test phase. There were 16 blocks of 12 randomly ordered trials (2 aspect ratios $\times$ 2 stimulus-types $\times$ 3 repetitions) during each of two testing sessions, with a variable rest period after the eighth block.

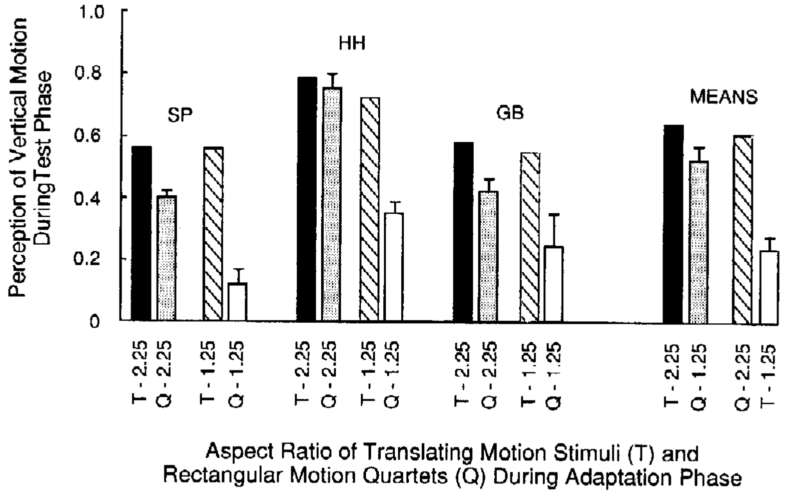



FIGURE 4. Experiment 2: the proportion of trials for which vertical motion was perceived anytime during the test phase (rectangular test quartets with an aspect ratio of 1.25) following adaptation with rectangular motion quartets or translational motion stimuli (adapting aspect ratios were 2.25 or 1.25). Data are reported only for trials during which horizontal motion was perceived for the entire adaptation phase. Standard errors of the difference between the translational and quartet stimuli for each subject (over sessions) and over subjects are indicated by error bars.

*Results*

Horizontal motion was perceived during the entire adaptation phase on 100% of the trials for the translational motion stimuli and the 2.25 aspect ratio quartet, and on an average of 54% of the trials for the 1.25 aspect ratio quartet. As in Experiment 1, vertical motion was perceived more often for the test quartet when the adapting quartet had a 2.25 compared with a 1.25 aspect ratio; the difference was substantially greater than the standard error of the difference for all three subjects (Fig. 4). In addition, vertical motion was perceived more often for the test quartets following adaptation to the translational stimuli compared with the motion quartets. This difference was large and reliable for the 1.25 adapting aspect ratio, which was consistent with the hypothesis that adaptation effects would be influenced by the activation of vertical motion detectors for the motion quartet. The translational/quartet difference was smaller for the 2.25 adapting aspect ratio (it was unreliable for one subject). This was consistent with the relatively weak activation of vertical motion detectors by the 2.25 aspect ratio adapting quartet and the minimal activation of vertical motion detectors by the horizontal, translational stimulus.

*Discussion*

Strong adaptation effects were obtained when only horizontal motion detectors were activated during adaptation; i.e., the perception of vertical motion was enhanced for the test stimulus following adaptation with the horizontal, translational stimuli. When it was possible for vertical motion detectors to be activated during the adaptation phase (especially for the 1.25 aspect ratio quartet, for which the vertical distance was similar to the horizontal distance between dot positions), the perception of vertical motion for the test stimulus decreased. This was the case even though the analysis was restricted to trials for which the activation of vertical detectors during adaptation was not sufficient for vertical motion to be perceived.

As indicated earlier, there are two explanations for why increasing the activation of vertical detectors during adaptation would reduce the effect of adaptation on the motion perceived during the test phase (the explanations are not mutually exclusive). (1) If horizontal and vertical detectors were similarly activated during the adaptation phase, they would be similarly adapted, so there would be no significant horizontal/vertical changes in detector sensitivity to influence perception during the subsequent test phase. (2) Activated vertical detectors could have reduced the activation of horizontal detectors because vertical and horizontal motion detectors are mutually inhibitory (Snowden, 1989); the greater the activation of vertical detectors, the greater the inhibitory suppression of horizontal detector activation during the adaptation phase, and therefore, the less the influence of the horizontal motion perceived during the adaptation phase on the motion perceived during the test phase.

It remained conceivable, however, that vertical detectors are as strongly activated for the 2.25 as for the 1.25 aspect ratio adapting quartet, but the quartets presented during the test phase were not appropriate for detecting the effects of vertical adaptation for the 2.25 aspect ratio. This possibility arises because the adapting and test stimuli were matched with regard to the horizontal, but not the vertical distance between dot positions on successive frames. Thus, the vertical detectors stimulated by the 2.25 adapting quartets may have differed from those stimulated by the 1.25 test quartets in terms of either their selectivity for different

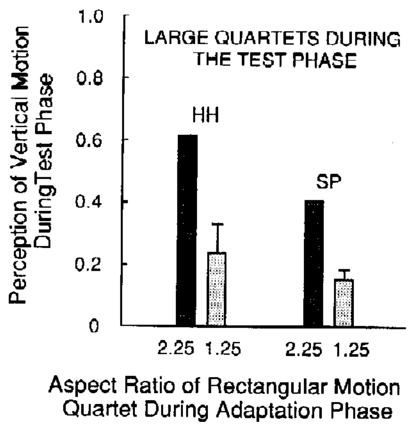



FIGURE 5. Experiment 2 (additional results): the proportion of trials for which vertical motion was perceived anytime during the test phase as a function of the aspect ratio (2.25 or 1.25) of the adapting quartets. The vertical inter-dot distance for the test quartet was matched to that of the adapting quartet with a 2.25 aspect ratio (the test quartet's aspect ratio was 1.29). Data are reported only for trials during which horizontal motion was perceived for the entire adaptation phase. Standard errors of the difference between the translational and quartet stimuli for each subject (over sessions) and over subjects are indicated by error bars.

spatial scales or different speeds. As a result, reductions in vertical detector sensitivity following adaptation to the 2.25 aspect ratio quartet may not have been observable for the 1.25 aspect ratio test quartet. An additional experiment addressed this possibility.

*Additional results*. The adapting stimuli were rectangular motion quartets with aspect ratios of 2.25 or 1.25; as before, the horizontal distance between dot positions was 6.4 min and the vertical distance was 14.4 or 8.0 min. The test quartet was modified in this experiment to match the 2.25 aspect ratio adapting quartet with regard to the 14.4 min vertical distance between dot positions (the horizontal distance between dot positions was increased to 11.2 min for the test quartet, resulting in an aspect ratio of 1.29). The experiment was otherwise identical to Experiment 2. If previously observed effects of adapting aspect ratio were an artifact of the 1.25 but not the 2.25 adapting quartet matching the 1.25 test quartet in terms of vertical distance between dot positions, the match now favors the 2.25 adapting quartet, so the reverse of the previous results should be obtained. That is, by this argument less vertical motion would be perceived for the enlarged test quartet following adaptation with the 2.25 compared with the 1.25 aspect ratio, because motion perception for the enlarged test quartet would be influenced only by adaptive reductions in the sensitivity of the vertical motion detectors activated by the 2.25 adapting aspect ratio.

The results, again analyzed only for trials in which horizontal motion was perceived for the entire adaptation phase, replicated previous evidence that the perception of vertical motion during the test phase was greater following adaptation with the 2.25 compared with the 1.25 aspect ratio quartet (Fig. 5). The observed effect of the adapting aspect ratio on the motion perceived for the test quartet could therefore be attributed to the same vertical motion detectors being differentially activated by the 2.25 and 1.25 aspect ratio adapting quartets, rather than different vertical detectors (with different spatial scale or speed selectivity) being activated by the adaptation and test quartets.*

*Effects associated with differences in selectivity for spatial scale or speed might be observable for larger differences between the dimensions of the adapting and test quartets.

## EXPERIMENT 3

The purpose of this experiment was to determine whether there is a relationship between the differential effect of the adapting quartet's aspect ratio on the motion perceived for the test quartet, and the differential effect of the quartet's aspect ratio on its stability. The preceding experiments indicate that adaptation effects depend on the relative activation of horizontal compared to vertical motion detectors during adaptation, and it is likely that the stability of the motion quartet also depends on the relative activation of horizontal compared to vertical detectors. Hock *et al.* (1993) have shown that the stability of the horizontal motion perceived for the motion quartet increases with the aspect ratio of the quartet; increasing the aspect ratio presumably increases the activational advantage of the horizontal motion detectors, making it less likely that random fluctuations favoring the perception of vertical motion could produce spontaneous changes in perceived motion direction.

In addition to aspect ratio, the stability of perceived motion varies with the temporal frequency with which motion quartets are presented (Kruse *et al.*, 1986). That is, higher temporal frequencies (briefer frame durations) result in a higher rate of spontaneous change between the perception of horizontal and vertical motion than lower temporal frequencies (longer frame durations). If adaptation effects are related to the stability of the adapting stimulus, a stronger adapting effect would be expected for motion quartets presented with longer frame durations.

### *Method*

Adaptation effects were measured as in the preceding experiments. In addition, the stability of the perceived horizontal motion was measured by determining the frequency with which horizontal motion that was perceived at the start of a trial spontaneously changes to vertical motion sometime later in the trial.

*Stimuli*. The adaptation trials had the same structure as in the preceding experiment. During the adaptation phase of each trial the aspect ratio of the rectangular quartet was 2.25 or 1.25 and the frame duration was 495 or 195 msec. During the test phase the aspect ratio was 1.25 and the frame duration 195 msec. Trials measuring the stability of the perceived horizontal motion were composed of nine uninterrupted display cycles with the rectangular

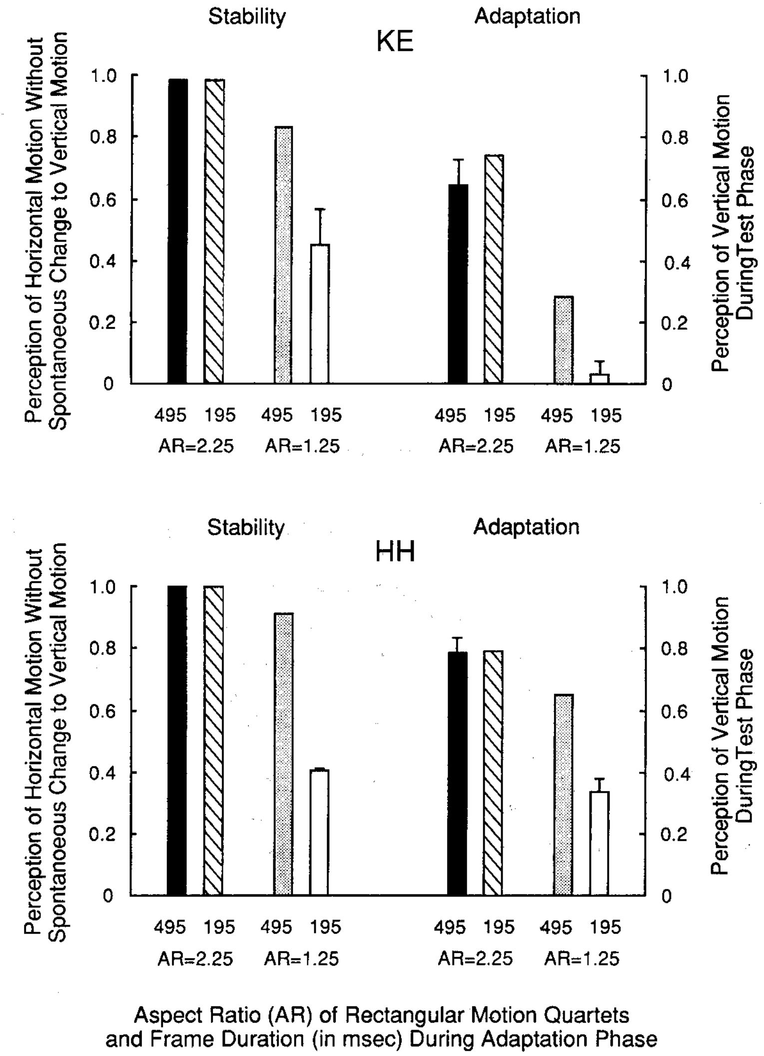



FIGURE 6. Experiment 3, stability measurements (ordinate on the left side of each graph): the proportion of trials for which there are *no* spontaneous changes to vertical motion after horizontal motion was perceived at the start of the trial (frame durations were 495 or 195 msec; aspect ratios were 2.25 or 1.25). Experiment 3, adaptation measurements (ordinate on the right side of each graph): the proportion of trials for which vertical motion was perceived anytime during the test phase following adaptation with rectangular motion quartets with frame durations of 495 or 195 msec (aspect ratios were 2.25 or 1.25 for the adapting quartets and 1.25 for the rectangular test quartet). Data are reported only for trials during which horizontal motion was perceived for the entire adaptation phase. Standard errors of the difference between the 495 and 195 msec frame durations for each subject (over sessions) and over subjects are indicated by error bars for both stability and adaptation measurements.

motion quartets. The aspect ratio was either 1.25 or 2.25, and the frame duration was either 195 or 495 msec.

*Procedure*. For trials measuring the adaptive effect of perceived horizontal motion, the first response at the end of a trial indicated whether horizontal motion was perceived during the entire adaptation phase and the second indicated whether vertical motion was perceived anytime during the test phase. For trials measuring the stability of perceived horizontal motion, the first response indicated whether the motion perceived at the start of each trial was horizontal and the second indicated whether a spontaneous switch to the perception of vertical motion occurred anytime later in the trial. There were three sets of 96 trials during each of two testing sessions, two measuring adaptation and a third, intervening set measuring stability, with a variable rest period between the sets. Each set of 96 consisted of 8 blocks of 12 randomly ordered trials (2 aspect ratios $\times$ 2 frame durations $\times$ 3 repetitions).

## *Results*

For the stability measurements, the motion perceived at the start of each trial was horizontal for all trials with the 2.25 aspect ratio and for 32 and 92% of the trials (for KE and HH, respectively) with the 1.25 aspect ratio. As in Chaudhuri & Glaser (1991), frame duration did not affect the frequency with which horizontal motion was perceived at the start of each trial for either aspect ratio.

However, as in Kruse *et al.* (1986), frame duration strongly affected the stability of the perceived horizontal motion once it was established. That is, when the aspect ratio was 1.25 (measured stability was at ceiling when it was 2.25), horizontal motion was perceived without spontaneous change to vertical motion more often for the 495 than the 195 msec frame duration (Fig. 6); the difference was much greater than the standard error of measurement for both subjects. As in Hock *et al.* (1993) and Hock & Voss (1990), perceived horizontal motion was more stable for the 2.25 than the 1.25 aspect ratio.

For the adaptation measurements, horizontal motion was perceived during the entire adaptation phase on every trial for the 2.25 adapting aspect ratio, on an average of 60% of trials for the 1.25 aspect ratio, 495 msec frame duration, and on an average of 50% of trials for the 1.25 aspect ratio, 195 msec frame duration. The effect of adapting to the motion quartets with the 195 msec frame duration was as in the preceding experiments; following adaptation phases during which only horizontal motion was seen, vertical motion was perceived more often during the test phase, when the adapting motion quartet had a higher aspect ratio (Fig. 6). However, for the 1.25 adapting aspect ratio, the perception of vertical motion during the post-adaptation test phase was greater when the frame duration during adaptation was 495 msec compared with when it was 195 msec (the difference was much greater than the standard error of the difference for both subjects). This effect of frame duration on the size of the adaptation effect was obtained despite the opposite result being favored by the potential selectivity of adaptation to the temporal frequency of the adapting quartet [Kruse *et al.* (1986) found that the adaptation effect was greater when the temporal frequency was the same during adaptation and test than when it differed].

### *Discussion*

The size of the adaptation effect in this and the preceding experiments was correlated with the stability of the horizontal motion perceived for the adapting quartet. This was the case regardless of whether the stability stemmed from the quartet's aspect ratio or frame duration. Stability predicts adaptation effects in this paradigm because both reflect the relative activation of horizontal vs vertical motion detectors.

## EXPERIMENT 4

The purpose of this experiment was to determine why the activation of vertical motion detectors influences adaptation, even though horizontal motion is perceived. As discussed in Experiment 2, both horizontal and vertical detectors could adapt; when the difference in their activation is small (the 1.25 aspect ratio quartet), they could adapt similarly, and changes in horizontal/vertical detector sensitivity would only minimally influence motion perception for the test quartet. A second possibility (which does not preclude the first) is that increased activation of vertical motion detectors during adaptation increases the inhibitory suppression of horizontal detector activation (Snowden, 1989), reducing the extent to which horizontal motion detectors adapt.

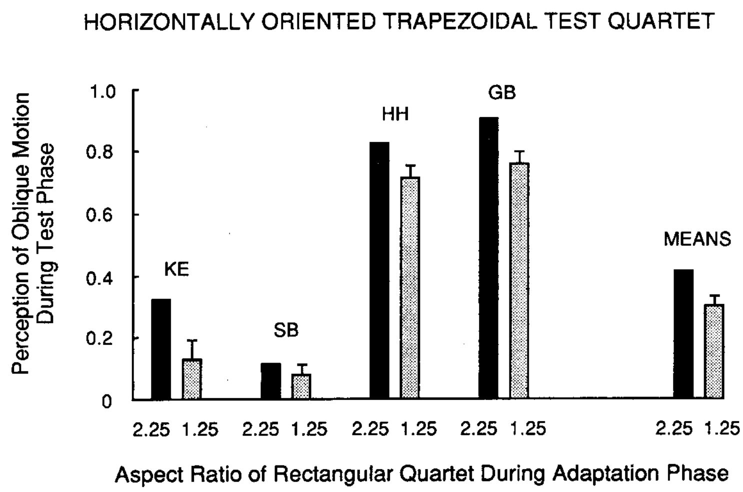
The adaptation of perceived horizontal motion and *un*perceived vertical motion were independently tested in this experiment by the presentation of trapezoidal test quartets (Fig. 1). For the horizontally oriented, trapezoidal quartet, the perception of either horizontal or oblique motion is possible; differences in the adaptation of horizontal motion detectors while perceiving horizontal motion for the rectangular adapting quartets were indicated by differences in the perception of oblique motion during the test phase. For the vertically oriented, trapezoidal test quartet, the perception of either vertical or oblique motion was possible; differences in the adaptation of vertical motion detectors while perceiving horizontal motion for the rectangular adapting quartets again were indicated by differences in the perception of oblique motion during the test phase (the possibility that the perception of oblique motion depends on the activation, and adaptation, of both vertical and horizontal motion detectors is addressed in Experiment 5).

### *Method*

*Stimuli.* The frame duration was 195 msec and the interval between the adapting (6 display cycles) and test (3 display cycles) phases of each trial was 495 msec. The adapting stimulus was a rectangular motion quartet with aspect ratio of 2.25 or 1.25; the horizontal distance between the dot positions was 6.4 min and the vertical distance was 14.4 or 8.0 min. Either the horizontally or vertically oriented, trapezoidal quartet was presented during the test phase. The distances between dot positions along the parallel short and long sides of the trapezoidal quartets were 3.2 and 16.0 min, the distance between the parallel sides was 6.4 min, and the oblique sides always formed a 45 deg angle with the parallel sides.* The centers of both adapting quartets corresponded with the center of the screen, and the centers of both test quartets were displaced 24 min from center in one of eight randomly selected directions. The "interrupting" stimulus at the end of each trial (to minimize possible inter-trial effects) was a single dot presented during each of 13 frames on a different corner of an imaginary 9.6 min square such that all possible horizontal, vertical, and oblique motion directions were perceived once.

*Procedure.* At the end of each trial subjects first indicated whether horizontal motion was perceived for the rectangular adaptation quartet during the entire adaptation phase, and then whether oblique motion was perceived for the trapezoidal quartet anytime during the test phase. There were two sets of 72 trials during each of four sessions (six for KE), one set with the horizontally

*The horizontal distances between dot positions for the horizontally oriented, trapezoidal quartet were increased by 1.6 min top and bottom for subject KE in this experiment (but not Experiment 5) since pilot work had suggested that horizontal motion for her would otherwise have been too dominant in relation to oblique motion.



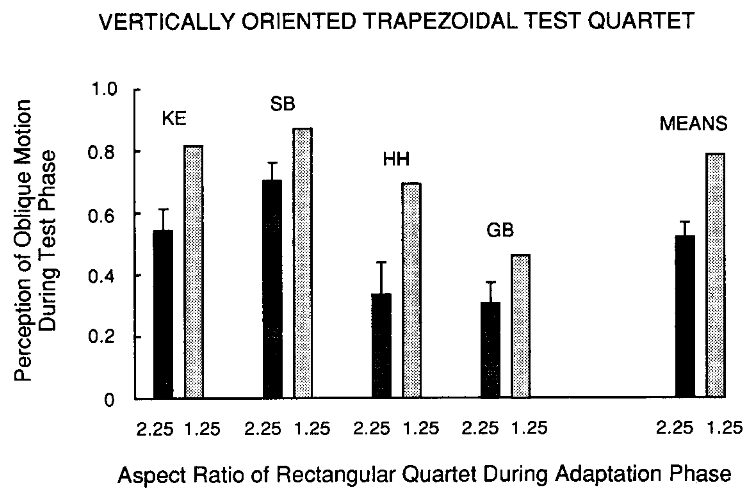




FIGURE 7. Experiment 4: the proportion of trials for which oblique motion was perceived anytime during the test phase (for either the horizontally or vertically oriented, trapezoidal quartets) as a function of the aspect ratio (2.25 or 1.25) of the rectangular adapting quartet. Data are reported only for trials during which horizontal motion was perceived for the entire adaptation phase. Standard errors of the difference between the 2.25 and 1.25 adapting aspect ratios for each subject (over sessions) and over subjects are indicated by error bars.

oriented and the other with the vertically oriented, trapezoidal test quartet, with a variable rest period between them (their order was alternated on successive sessions). Each set of 72 trials consisted of four blocks of 18 randomly ordered trials (2 adapting aspect ratios × 9 repetitions).

### *Results*

Averaging over the four participating subjects, horizontal motion was seen for the entire adapting phase on 98% of the trials when the adapting rectangular quartet had an aspect ratio of 2.25, and on 60% of the trials when the adapting quartet had an aspect ratio of 1.25. The proportion of trials for which oblique motion was perceived for the trapezoidal test quartets was determined on the basis of these trials.

When the orientation of the trapezoidal test quartet was horizontal, so either oblique or horizontal motion could be seen, oblique motion was perceived more often when the rectangular adapting quartet's aspect ratio was 2.25 compared with when it was 1.25 (top of Fig. 7). This difference, which was reduced in size for SB (probably because of floor effects), was substantially greater than the standard error of the difference for the other subjects. It indicated that the adaptation of horizontal motion detectors was greater for the 2.25 than the 1.25 adapting aspect ratio.

When the orientation of the trapezoidal test quartet was vertical, so either oblique or vertical motion could be seen, oblique motion was perceived more often when the aspect ratio of the rectangular adapting quartet was 1.25 compared with when it was 2.25 (bottom of Fig. 7). This difference was substantially greater than the standard error of the difference for all four subjects, indicating that the adaptation of vertical motion detectors was greater for the 1.25 than the 2.25 adapting aspect ratio.

*Discussion*

The results for the horizontally oriented, trapezoidal test quartets indicate that horizontal motion detectors were more strongly activated for the 2.25 than the 1.25 adapting aspect ratio. Since horizontal motion was established over the same displacement for both aspect ratios, the difference in horizontal detector activation must have been due to inhibition from activated vertical motion detectors. The greater activation of vertical motion detectors for the 1.25 than the 2.25 adapting aspect ratio would result in a greater inhibitory reduction in the activation of horizontal motion detectors for the 1.25 aspect ratio, accounting for the smaller adaptive reduction in horizontal detector sensitivity for the 1.25 compared with the 2.25 adapting aspect ratio (and thus, less perception of oblique motion for the trapezoidal test quartet).

The results for the vertically oriented, trapezoidal test quartets indicate that there was less perception of vertical motion following adaptation to the 1.25 compared with the 2.25 aspect ratio. Thus, there was adaptation of vertical motion, even when vertical motion was not perceived during the adaptation phase. The activation of vertical motion detectors was stronger for the 1.25 compared with the 2.25 aspect ratio, so sensitivity to vertical motion was more reduced by adaptation to the 1.25 aspect ratio (and there was more perception of oblique motion for the trapezoidal test quartet).

Thus, both possibilities considered in the introduction to this experiment were supported by its results. That is, unperceived vertical motion as well as perceived horizontal motion adapted, and the adaptation of horizontal motion was reduced as a result of inhibitory influences from activated vertical motion detectors.

## EXPERIMENT 5

An alternative account of the results obtained in Experiment 4 for the vertically oriented, trapezoidal test quartet assumes that the perception of oblique motion depends on the activation of *both* vertical and horizontal motion detectors. That is, rather than the differential adaptation of unperceived vertical motion, it could be argued that oblique motion was more frequently perceived following adaptation to the 1.25 compared with the 2.25 rectangular quartet because of the greater reduction in sensitivity to the perceived horizontal motion for the 2.25 adapting aspect ratio. The loss in sensitivity to its horizontal component would presumably be reflected in the reduced perception of oblique motion for the trapezoidal test quartets.

The purpose of this experiment was to demonstrate that the componential view of oblique motion cannot account for the adaptation effects observed in Experiment 4, and in doing so, to provide further evidence for the adaptation of unperceived motion directions that compete with motion directions that are perceived. To do so, we effectively reversed the trial structure of Experiment 4. Now the adapting stimuli were horizontally or vertically oriented, trapezoidal quartets (randomly mixed), and the test stimulus was a neutral, rectangular motion quartet. Only the results of trials for which oblique motion was perceived during the entire adaptation phase were evaluated (regardless of the orientation of the trapezoidal adapting quartet).

It was anticipated that vertical motion would adapt for the vertically oriented, trapezoidal quartets and horizontal motion would adapt for the horizontally oriented, trapezoidal quartets, even when only oblique motion was perceived during the adaptation phase of each trial. As a result, the perception of vertical motion for the subsequently presented, rectangular test quartet would be greater following the perception of oblique motion for the horizontally oriented, trapezoidal adapting quartet (unseen horizontal motion adapts) compared with the vertically oriented, trapezoidal adapting quartet (unseen vertical motion adapts).

According to the alternative, componential view of oblique motion perception, both vertical and horizontal detectors would be equally activated for both trapezoidal quartets presented during adaptation (they differed by only a 90 deg rotation), so there would be no difference in their effect on the subsequently presented test quartet.

*Method*

*Stimuli.* The structure of each trial was identical to the three preceding experiments. The adapting stimulus was either a horizontally or vertically oriented, trapezoidal quartet, and the test stimulus was a rectangular quartet with an aspect ratio of 1.25 (their dimensions were as in Experiment 4). The first response at the end of each trial indicated whether oblique motion was perceived for the trapezoidal quartet during the *entire* adaptation phase; the second indicated whether vertical motion was perceived for the rectangular motion quartet anytime during the test phase. There were 16 blocks of 14 trials (2 orientations of the adapting quartet $\times$ 7 repetitions) during each of three testing sessions, with a variable test period after the eighth block.

*Results*

Averaging over the three subjects, the frequency with which oblique motion was perceived during the entire adaptation phase was similar for the vertically oriented (54% of the trials) and horizontally oriented, trapezoidal quartets (59% of the trials). These frequencies reflect the relatively low stability of the perceived oblique motion. When oblique motion was perceived at the start of the adaptation phase, there were frequent spontaneous changes to either horizontal or vertical motion, depending on the orientation of the trapezoidal quartet. The proportion of trials for which vertical motion was perceived for the rectangular test quartet was determined on the basis of the trials for which oblique motion was perceived for the entire adaptation phase.

Vertical motion was perceived during the test phase

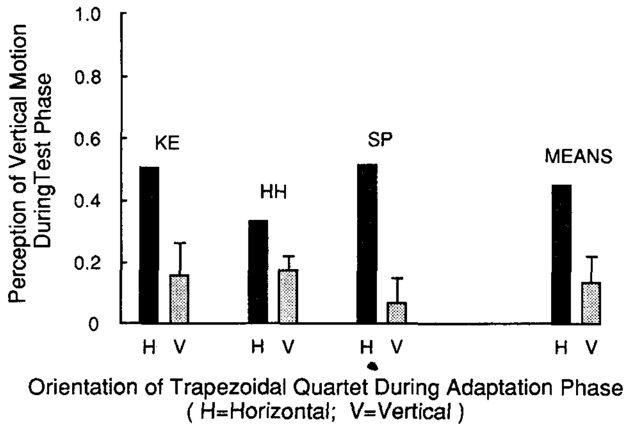



FIGURE 8. Experiment 5: the proportion of trials for which vertical motion was perceived anytime during the test phase (the rectangular test quartet had an aspect ratio of 1.25) following adaptation with either horizontally or vertically oriented, trapezoidal quartets. Data are reported only for trials during which oblique motion was perceived for the entire adaptation phase. Standard errors of the difference between the horizontally and vertically oriented, trapezoidal adapting quartets for each subject (over sessions) and over subjects are indicated by error bars.

more often following adaptation to the horizontally than to the vertically oriented, trapezoidal quartet; the difference was substantially greater than the standard error for all three subjects (Fig. 8). In addition to ruling out an account of Experiment 4's results based on a componential view of oblique motion perception (no differences in adaptation would be expected for the two orientations of the adapting quartet), the results provided further and direct evidence for the adaptation of unperceived motion directions that compete with the motion directions that are perceived during the adaptation phase.

## GENERAL DISCUSSION

The experiments reported in this article indicate the following. (1) Vertical motion detectors are activated while horizontal motion is perceived for the motion quartet. This conclusion follows from the reduction of the adaptive effect of the horizontal motion perceived for adapting rectangular quartets by the activation of vertical motion detectors. Otherwise there would have been no difference in Experiment 2 between the adapting effects of the horizontal motion perceived for rectangular motion quartets (vertical motion perception was possible) and matching translational stimuli (only the perception of horizontal motion was possible). (2) The relative activation of horizontal and vertical detectors depends on the aspect ratio of the motion quartet. Otherwise there would have been no effect of the adapting aspect ratio on the size of the adaptation effect (Experiment 1). (3) The activation of horizontal motion detectors is reduced by inhibitory interactions with activated vertical motion detectors. Otherwise, there would have been no difference in the perception of oblique motion for the horizontally oriented, trapezoidal test quartet as a function of the adapting aspect ratio (Experiment 4). (4) *Un*perceived (but possible) motion directions can adapt, depending on the relative activation of horizontal and vertical motion detectors. Otherwise, there would have been no difference in the perception of oblique motion for the vertically oriented, trapezoidal test quartet as a function of the adapting aspect ratio (Experiment 4), nor would it have mattered whether horizontal or vertical motion was *un*perceived while oblique motion was being perceived for trapezoidal adapting quartets (Experiment 5). (5) The extent to which adaptation is selective to the perceived motion is predicted by the stability of the adapting quartet.

The horizontal motion perceived for rectangular quartets with large aspect ratios is very stable. Spontaneous changes to the perception of vertical motion are much less likely than is the case for rectangular quartets with aspect ratios closer to one. The stability of the adapting quartet predicts whether adaptation will be selective to the perceived motion direction, because stability as well as selectivity in adaptation depend on the relative activation of horizontal and vertical detectors.

When the activation of horizontal detectors is substantially greater than the activation of vertical detectors, the perceived horizontal motion is stable because random fluctuations favoring vertical motion are unlikely to overcome the activational advantage of the horizontal motion detectors.* Adaptation effects are then selective to the perceived horizontal motion because vertical motion detectors are relatively "insulated" from the effects of adaptation when their activation levels are low (inhibitory competition further suppressing their activation). The sensitivity of horizontal detectors is therefore reduced much more than the sensitivity of vertical detectors, and the persistence of these differences in sensitivity until the test phase of each trial results in substantial enhancement of vertical motion perception for the test quartets. However, the adapting quartet becomes less stable when the activation levels of horizontal and vertical motion detectors are more similar. The sensitivities of horizontal and vertical detectors are then reduced similarly by adaptation, which is now *not* selective to the motion perceived during adaptation, so relatively little perception of vertical motion is observed for the test quartets compared with when horizontal and vertical detectors are differentially adapted.

The value of stability as a predictor of selectivity in adaptation is indicated by the results of Experiment 3. It

*Schöner & Hock (1995) have developed a nonlinear, dynamical model in which the relative 'strength' of competing motions (Burt & Sperling, 1981) is treated as a parameter that controls the "intrinsic forces" which influence the formation of horizontal and vertical motion patterns for motion quartets. The model demonstrates that differences in the relative stability of perceived motion patterns can emerge from competitive interactions, through which the visual system is presumed to establish apparent motion correspondences (Ullman, 1979).

remains uncertain why frame duration (temporal frequency) would affect the relative activation of horizontal and vertical motion detectors, so without knowledge of its effects on perceptual stability (Kruse *et al.*, 1986), there would have been no *a priori* basis for expecting frame duration to influence whether adaptation is selective to the motion directions perceived during the adaptation interval (selective adaptation of horizontal motion detectors was indicated by increased perception of vertical motion for the test quartet following adaptation to the 1.25 aspect ratio quartet with 495 compared to 195 msec frame durations).

In conclusion, the results of this study suggest a separation between the activation (and adaptation) of motion detectors and the actual perception of motion. This is consistent with Logothetis and Schall's (Logothetis & Schall, 1989) observations of directionally selective neurons in the superior temporal sulcus of monkeys. They found that the response of some neurons to gratings moving in their preferred direction was suppressed when a binocularly rivalrous grating moving in the opposite direction determined the perceived motion direction; the response of other neurons depended only on whether they were stimulated by a grating moving in their preferred direction, regardless of the motion direction that was perceived. That stability-predicted adaptation can be obtained for unperceived as well as perceived pattern features indicates that adaptation occurs prior to the determination of which activated pattern features will be realized in perceptual experience.

## REFERENCES


Anstis, S. M., Giaschi, D. & Cogan, A. I. (1985). Adaptation to apparent motion. *Vision Research, 25*, 1051–1062.

Ball, K. B., Sekuler, R. & Machamer, J. (1983). Detection and identification of moving targets. *Vision Research, 23*, 229–238.

Blakemore, C. & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology, 203*, 237–260.

Burt, P. & Sperling, G. (1981). Time, distance, and feature trade-offs in visual apparent motion. *Psychological Review, 88*, 171–195.

Chaudhuri, A. & Glaser, D. A. (1991). Metastable motion anisotropy. *Visual Neuroscience, 7*, 397–407.

Finlay, D. & Von Grünau, M. (1987). Some experiments on the breakdown effect in apparent motion. *Perception and Psychophysics, 42*, 526–534.

Girgus, J. J., Rock, I. & Egatz, R. (1977). The effect of knowledge of reversibility on the reversibility of ambiguous figures. *Perception and Psychophysics, 22*, 550–557.

Hochberg, J. E. (1950). Figure–ground reversal as a function of visual satiation. *Journal of Experimental Psychology, 40*, 682–686.

Hock, H. S., Kelso, J. A. S. & Schöner, G. (1993). Bistability and hysteresis in the organization of apparent motion patterns. *Journal of Experimental Psychology: Human Perception and Performance, 19*, 63–80.

Hock, H. S. & Voss, A. (1990). Spontaneous pattern changes for bistable stimuli: Evidence against neural satiation. Paper presented at the 31st meeting of the Psychonomic Society, New Orleans, LA.

Kruse, P., Stadler, M. & Wehner, T. (1986). Direction and frequency specific processing in the perception of long-range apparent motion. *Vision Research, 26*, 327–335.

Levinson, E. & Sekuler, R. (1975). Inhibition and disinhibition of direction-specific mechanisms in human vision. *Nature, 254*, 692–694.

Logothetis, N. K. & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science, 245*, 761–763.

Maffei, L., Fiorentini, A. & Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science, 182*, 1036–1038.

Mueller, C. G. (1951). Frequency of seeing functions for intensity discrimination at various levels of adapting intensity. *Journal of General Physiology, 34*, 463–474.

Nawrot, M. & Blake, R. (1989). Neural integration of information specifying structure from stereopsis and motion. *Science, 244*, 716–718.

Pantle, A. J. & Sekuler, R. (1968). Size detecting mechanisms in human vision. *Science, 162*, 1146–1148.

Pantle, A. J. & Sekuler, R. (1969). Contrast response of human visual mechanisms sensitive to orientation and direction of motion. *Vision Research, 9*, 397–406.

Schöner, G., & Hock, H. S. (1995). Concepts for a dynamical theory of perceptual organization: An example from apparent movement. In P. Kruse & M. Stadler (Eds), *Multistability in perception*. Berlin: Springer.

Sekuler, R. & Ganz, L. (1963). A new aftereffect of seen movement with a stabilized retinal image. *Science, 139*, 1146–1148.

Snowden, R. J. (1989). Motions in orthogonal directions are mutually suppressive. *Journal of the Optical Society of America A, 6*, 1096–1101.

Ullman, S. (1979). *The interpretation of visual motion*. Cambridge, MA: MIT Press.

Walraven, J., Enroth-Cugell, C., Hood, D. C., MacLeod, D. I. A. & Schnapf, J. L. (1990). The control of visual sensitivity: Receptoral and postreceptoral processes. In Spillman, L & Werner, J. S. (Eds), *Visual perception: The neurophysiological foundations*. New York: Academic Press.


*Acknowledgements*—We are grateful to Robert Shapley, Betty Tuller, and two anonymous reviewers for their insightful comments. The research was supported in part by Deutsche Forshungsgemeinschaft DFG Scho-336-4-2 and DFG Scho-336-3-1, and the Smith Family Laboratory for Collaborative Research in Psychobiology.